Empirically Derived Survival Rates of a Native Mussel, Amblema plicata, in the Mississippi and Otter Tail Rivers, Minnesota

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ABSTRACT.—We used a mark-recapture method to measure survival of a native unionid mussel, *Amblema plicata*, at sites with low, moderate and high zebra mussel (*Dreissena polymorpha*) densities (mean values ± SE equaled 0.4 ± 0.2, 50.5 ± 13 and 1750 ± 260 individuals/m² respectively) in the Mississippi River, Minnesota, and at one site without *D. polymorpha* in the Otter Tail River, Minnesota. In 1996 240 *A. plicata* from each site were uniquely marked. In 1997, 1998, 1999 and 2000 marked mussels were recovered; identified; survival determined; and, if alive, they were returned to the substratum. Mean annual survival differed significantly among sites (χ^2 = 4.08, df 3, P < 0.0001). Mean annual survival rates in the Mississippi River's low infestation population (LOW) were 99 ± 0.3%, and 89 ± 1.2% in the moderately infested population (MOD), while survival at the highly infested population (HIH) was 65 ± 7.8%. Mean annual survival for the Otter Tail River population (REF) of *A. plicata* was 98 ± 0.5%. Results demonstrated that *A. plicata* has high mean annual survival (>97%) in natural habitats that are not colonized by *D. polymorpha* and the survival rates decline significantly relative to increases in *D. polymorpha* densities.

INTRODUCTION

Zebra mussels (*Dreissena polymorpha*) (Pallas 1771), introduced to North America from Europe in the 1980s (Hebert *et al.*, 1989), are considered a major threat to native mussel populations (Ricciardi *et al.*, 1998). Evidence of the effects of zebra mussels on native mussels has been based on correlations between increased abundance of *D. polymorpha* and decreased abundance of native species (Haag *et al.*, 1993; Gillis and Mackie, 1994; Ricciardi *et al.*, 1995, 1998; Schloesser *et al.*, 1996, 1998). However, native mussels had been declining in much of North America since the early 1900s, long before the appearance of *D. polymorpha*, with losses attributed to commercial harvest, water pollution and habitat degradation (Smith, 1919; Thiel, 1981; Williams *et al.*, 1993). In many locations, these threats to native mussels are present in addition to *D. polymorpha*, and it is impossible to isolate the effect of *D. polymorpha* alone using correlative evidence. This concern over the loss of native mussels due to *D. polymorpha* colonization (Haag *et al.*, 1993; Gillis and Mackie, 1994; Nalepa, 1994; Ricciardi *et al.*, 1995, 1998) suggested to us the necessity and urgency for direct measurements of native mussel survival, stimulating the initiation of this study.

However, the measurement of survival rates in populations of most animals is extremely

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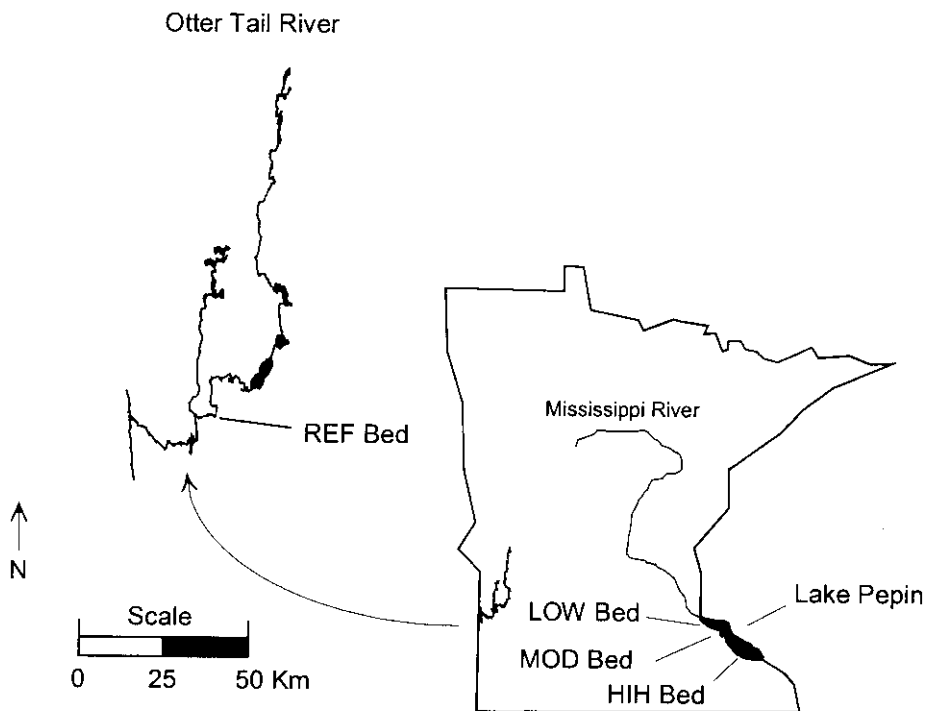
FIG. 1.—Map of the locations where the mark-recapture populations of *Amblema plicata* were located in the Mississippi and Otter Tail rivers, Minnesota

difficult, generally indirect and frequently unreliable (Menkens and Boyce, 1993). Commonly used indirect methods, such as "life tables" and "catch curves" involve untestable assumptions such as population stability and a stationary population (D. Anderson, Colorado State University, pers. comm.), typically incorporate complex statistical models and may require large samples of tagged individuals in multiple categories such as different age groups (Menkens and Boyce, 1993). Therefore, we chose a direct measurement of survival using a mark-recapture study design and recorded the fate of marked individuals for several years (Otis *et al.*, 1978; Seber, 1982).

The objectives of this study were to determine survival rates of native mussel populations in natural habitat without *Dreissena polymorpha* and in areas colonized by *D. polymorpha*. Lake Pepin, a natural widening of the upper Mississippi River at the southeastern border of Minnesota with Wisconsin, provided an opportunity to directly measure survival of native mussels in their native habitats and in the presence of varying densities of *D. polymorpha*. A reference population was also selected in the Otter Tail River in west central Minnesota where *D. polymorpha* does not yet occur.

We report mean annual survival rates of a native species of mussel in areas not presently colonized with *Driessena polymorpha* and compare them to survival rates measured in locations currently colonized by varied densities of *D. polymorpha*.

METHODS

Study areas.—This study was initiated in 1995 in the Mississippi and Otter Tail rivers, Minnesota (Fig. 1). Seven mussel beds that had been quantitatively sampled in Lake Pepin,

Mississippi River in the summer of 1995 (Hart, 1999) were categorized as having either low (LOW, 0–10 individuals/m²), moderate (MOD, 25–100 individuals/m²), or high (HIH, >250 individuals/m²) densities of *Dreissena polymorpha.* One bed from each category was selected for study. LOW, MOD and HIH infested populations were located at Methodist Point (River Mile, RM 779), Hok Si La (RM 776) and King's Coulee (RM 767), respectively (Fig. 1). Densities of *D. polymorpha* at the LOW, MOD and HIH beds averaged 0.4 ± 0.2, 50.5 ± 13 and 1750 ± 260 individuals/m², respectively (Hart, 1999). The Otter Tail River population (REF) was randomly selected from a pool of mussel beds known to have *Amblema plicata* (Say 1817) population densities similar to those in Lake Pepin but lacking *D. polymorpha* (Hart, 1995, 1999).

Mussel marking and recapture.—During the summer of 1996, 240 *Amblema plicata* (960 total) were collected by divers using scuba at each mussel bed. Mussels were held at the substrate water interface in mesh bags tied to the work boat. During processing mussels were held on the boat in 20-liter pails of water. Water in the pails was exchanged after every 10 mussels were processed to minimize stress. Maximum shell length and height were measured for each mussel, and individuals were marked with a predetermined code etched into the right valve of the shell using a battery-operated Dremel® tool. If *D. polymorpha* were attached to the marked native mussels, they were counted and left on the individual.

Marked mussels were placed in open corrals at each site. Corrals were primarily designed to assist the diver in relocating marked mussels, while still allowing for movement of unionids within a reasonably confined area. The corrals were constructed from 20, 10 cm high × 60 cm diameter fences cut from plastic barrels and attached to a 240 cm × 600 cm wooden frame. One frame per site was anchored to the river bed with concrete blocks and 12 marked *Amblema plicata* were hand placed in each of the 20 corrals attached to the frame. Site locations were recorded with a global positioning system.

During July or August 1997 and 1998, and 2000 at the MOD and REF sites, and July or August 1997, 1998, 1999 and 2000 at the LOW and HIH sites, marked mussels were recovered by divers and returned to the boat. Mussels were identified by their unique numbers and measured for shell length and height. If the mussel was alive, it was returned to the corral. Unfortunately, we were unable to recover marked mussels from the MOD and REF sites in 1999 because of expense and time constraints.

Data analysis.—Survival rates for marked mussels were calculated using the software program MARK (White and Burnham, 1999), a commercially available program obtainable without cost from Colorado State University's website. We used the Burnham model contained in MARK that uses information from both encounters of live and dead marked animals (White and Burnham, 1999), as well as information from missing individuals. This method estimates the fidelity, *i.e.,* the probability that the animal remains in the area and is available for recapture (White and Burnham, 1999). Therefore, this model allows for the estimate of the survival probability and not apparent survival as is the case when using only live recapture data (White and Burnham, 1999). Survival rates were compared among sites using chi-square tests (Sauer and Williams, 1989) and sequential Bonnferoni, *a-posteriori* adjusted comparisons (Rice, 1990).

In our analysis mussels that were not collected again after initial marking were not used in the survival calculations. However, mussels that were missing after initial marking and subsequently found after 1, 2, or 3 y were included in the analysis. Therefore, the survival rates we report are calculated on those mussels collected throughout the study using the joint Burnham model in program MARK (White and Burnham, 1999).

To alleviate our own concerns about how the exclusion of the missing mussels may have affected the calculation of survival rates, we took the advice of G. White (Colorado State
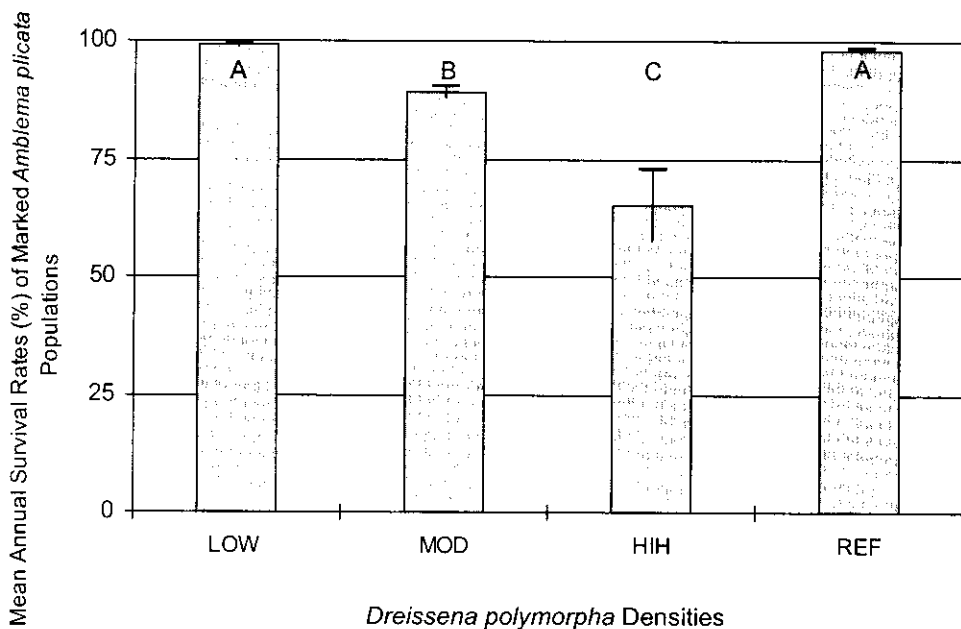
FIG. 2.—Comparisons between mean annual survival rates of *Amblema plicata* populations as a function of low (LOW, 0–10 individuals/m²), moderate (MOD, 25–100 individuals/m²), high (HIH, >250 individuals/m²) or no (REF) *Dreissena polymorpha* colonization densities from 1996–2000. Similar letters above histograms indicate a lack of significant differences among LOW, MOD, HIH or REF populations (mean ± SE; chi-square test, P > 0.05)

University, pers. comm.) and performed an additional analysis which included the missing individuals. There was no difference in the survival rates measured, whether missing individuals were included or not, while using the joint Burnham model (White and Burnham, 1999). Therefore, our approach of not including the missing mussels in the calculations was deemed acceptable (G. White, pers. comm.). It should be noted, however, that the recapture rates we report were calculated using data for all of the mussels that were originally marked at the beginning of the study.

To test for differences in size distributions of marked *Amblema plicata* among sites, mussels were assigned to one of three size groups based on initial shell length: small ($\leq$72 mm), medium ($73 < \times \leq 84$ mm) or large (>84 mm). Differences in size distributions of marked *A. plicata* among study beds were tested by calculating chi-square statistics from R × C contingency tables (Zar, 1984). To maintain an overall error rate of 0.05, P-values for each chi-square test and comparison of survival rates and size distributions were adjusted with a sequential Bonnferoni correction (Rice, 1990).

RESULTS

Mean annual survival and recapture of *Amblema plicata* was high (>89%) for all of the mussel populations we measured with the exception of the HIH bed. Mean annual survival rates were different among sites, averaging 99 ± 0.3% for the LOW population, 89 ± 1.2% for the MOD population and 98 ± 0.5% for the REF population, while survival averaged 65.2 ± 7.8% for the HIH population ($\chi^2 = 84.08$, df 3, P < 0.0001) (Fig. 2).

TABLE 1.—Inter-year survival probabilities of marked *Amblema plicata* in the Mississippi and Otter Tail rivers under varying *Dreissena polymorpha* densities

	Mussel Bed			
Year	LOW	MOD[a]	HIH	REF[a]
Survival Probabilities (SE)[b]				
1996–1997	1.000 (0.000)	0.978 (0.009)	0.879 (0.023)	1.000 (0.000)
1997–1998	0.955 (0.013)	0.934 (0.016)	0.596 (0.041)	0.966 (0.012)
1998–1999	1.000 (0.000)		0.608 (0.063)	
1999–2000	0.982 (0.007)	0.716 (0.021)	0.526 (0.096)	0.979 (0.009)
Mean Annual				
1996–2000	0.993 (0.003)	0.892 (0.012)	0.652 (0.078)	0.981 (0.005)

[a] Data are missing for 1998–1999 because of logistical constraints. However, the joint Burnham model we used to calculate survival rates accounts for these missing data during calculations (White and Burnham, 1999)

[b] Standard errors (SE) of the survival probabilities are enclosed in parenthesis

There was no significant difference in mean annual survival between the LOW and the REF beds ($\chi^2 = 2.94$, df 1, P = 0.09). In contrast, mean annual survival rates were significantly different between the LOW and MOD beds ($\chi^2 = 65.36$, df 1, P < 0.0001) and the REF and MOD beds ($\chi^2 = 47.93$, df 1, P < 0.0001), while mean annual survival was significantly lower at the HIH bed compared to the LOW bed ($\chi^2 = 18.97$, df 1, P < 0.0001), REF bed ($\chi^2 = 17.83$, df 1, P = 0.0001) and MOD bed ($\chi^2 = 9.25$, df 1, P = 0.002) (Fig. 2). Survival rates within the HIH and MOD populations began to decline only 2 y after initial marking (Table 1).

Recapture rates of *Amblema plicata* from the LOW, MOD and REF populations averaged 98%, while the recapture rate for the HIH population equaled 85%. The probability of mussels remaining in the area and available for recapture, *i.e.*, fidelity, was also high at all of the beds (>95%), indicating that the mussels did not tend to emigrate, or be taken (*e.g.*, by predators) from the marking sites.

We tested for differences in size distributions of the marked mussels among sites. This analysis was done to determine if size, an indicator of age, influenced survival. Size distributions of marked mussels were not significantly different for the LOW and HIH mussel populations ($\chi^2 = 1.38$, df 2, P = 0.50) (Fig. 3). Size distributions were significantly different for the LOW and MOD populations ($\chi^2 = 32.65$, df 2, P < 0.0004) and the MOD and HIH populations ($\chi^2 = 18.62$, df 2, P < 0.0004), whereas the REF population's size distributions were significantly different from all other populations (P < 0.0005) (Fig. 3).

Because the concern over the effects of *Dreissena polymorpha* on native mussels stimulated this research, the differing survival rates among the mussel beds with and without *D. polymorpha* colonies prompted us to investigate the abundance of *D. polymorpha* colonized on each *Amblema plicata* within the populations. The average number of *D. polymorpha* attached to marked *A. plicata* (colonization rates) at the LOW and MOD populations was significantly less than the HIH population in all years, whereas the number of *D. polymorpha* attached to marked *A. plicata* at the LOW population was significantly less than the MOD population in 1998 and 2000 (ANOVA and Tukey's multiple comparison tests, F = 181.14, df 12, 2604, P < 0.001) (Fig. 4). Also, due to the large increase in the numbers of *D. polymorpha* attached to the marked *A. plicata* at the HIH population in 2000, we were unable to count the actual numbers of *D. polymorpha* colonized upon them with out the
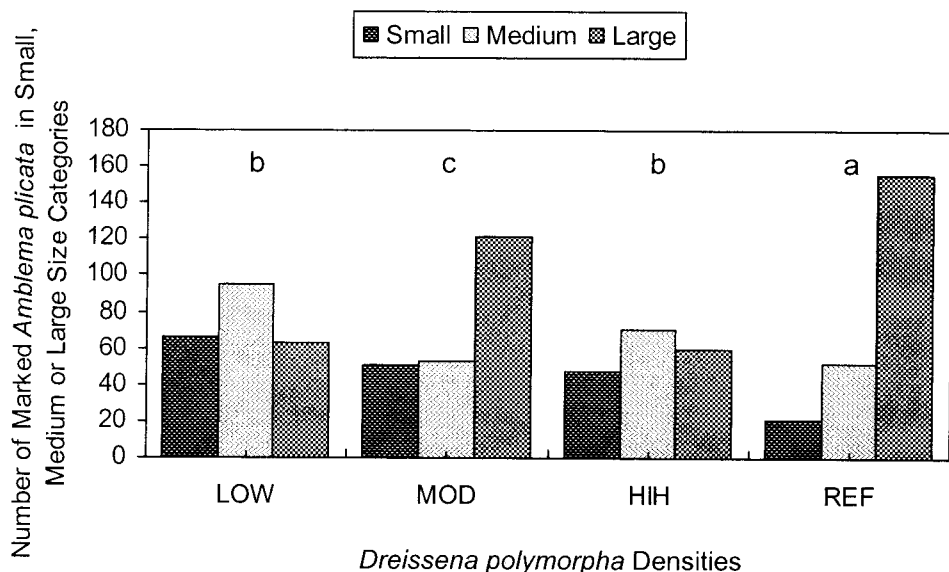
FIG. 3.—Comparisons of relative size distributions (small (≤72 mm), medium (73 < X ≤ 84 mm), large (>84 mm)) among marked *Amblema plicata* populations. Similar letters above histograms indicate a lack of significant differences among LOW, MOD, HIH or REF populations (chi-square test, P > 0.05)

possibility of inadvertently removing them. Using a comparable sized subsample we estimated the numbers of *D. polymorpha* attached to the marked *A. plicata* at the HIH population in 2000. Therefore, we did not include standard error bars for the number of *D. polymorpha* attached to *A. plicata* at the HIH population in 2000 (Fig. 4).

DISCUSSION

Using a mark-recapture study design we directly measured the survival rates of three populations of *Amblema plicata* in Lake Pepin, Mississippi River, and one population of *A. plicata* in the Otter Tail River. Mean annual survival rates for the four *A. plicata* mussel populations ranged from 65 ± 7.8 to 99 ± 0.3% among the four years of study. In habitats of the Mississippi and Otter Tail rivers subjected to low numbers of or no *Dreissena polymorpha*, mean annual survival of *A. plicata* was high for the 4 y of this study and was not significantly different between the LOW and REF populations (>97%, χ^2 = 2.94, df 1, P = 0.09). Survival rates declined significantly with an increase in *D. polymorpha* colonization. Mean annual survival of *A. plicata* was significantly lower at the HIH bed (65%) compared to all other mussel populations (>89%) studied (χ^2 = 84.08, df 3, P < 0.0001).

The population of *Amblema plicata* with the lowest mean annual survival (65 ± 7.8%), located at the HIH bed, coincided with the highest population densities of *Dreissena polymorpha* within Lake Pepin (Hart, 1999) and had the greatest numbers of *D. polymorpha* attached to the marked individuals. Additionally, mean annual survival rates were statistically the same at the LOW and REF populations, even though they differed slightly in size distributions. The size distributions of marked mussels at the REF and MOD beds were different from both the HIH and LOW beds, yet the *A. plicata* at the REF and MOD beds
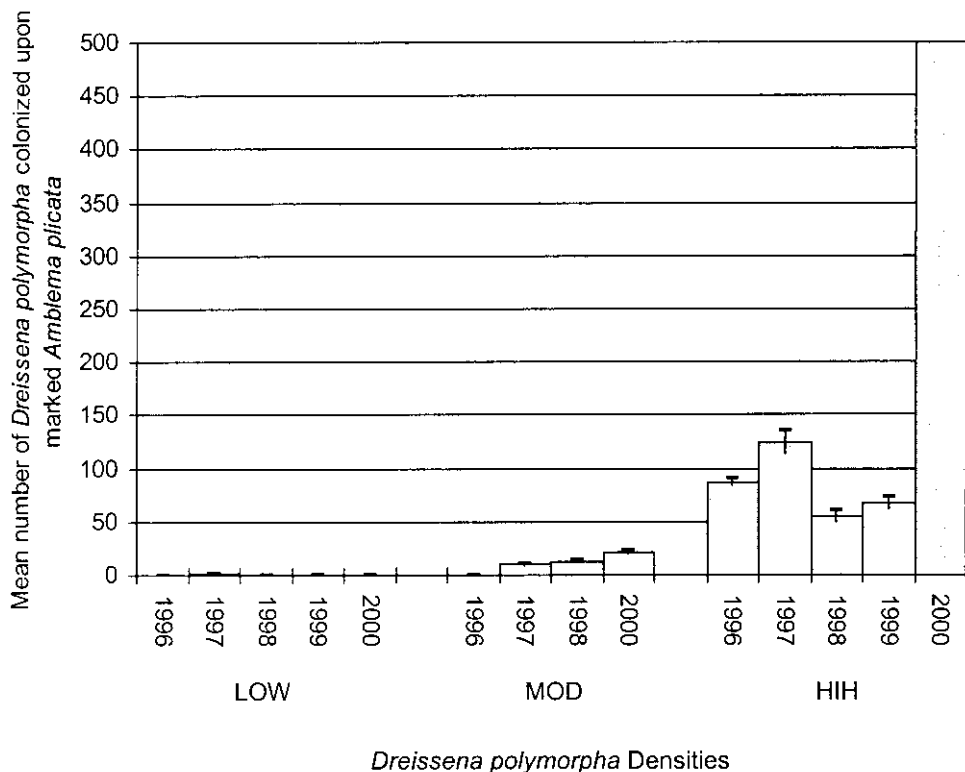
Dreissena polymorpha Densities

Fig. 4.—Colonization rates (the mean number of *Dreissena polymorpha/Amblema plicata*) of *D. polymorpha* upon marked *A. plicata* from 1996–2000. Values are the mean (± SE) number of *D. polymorpha/*marked *A. plicata*. Marked *A. plicata* and *D. polymorpha* were not retrieved from the MOD population in 1999 due to logistical constraints. Standard errors are not presented for *D. polymorpha* colonization rates at the HIH population for 2000 because the large number of *D. polymorpha* present upon the marked *A. plicata* prevented counts. Colonization rates of *D. polymorpha* for the HIH population during 2000 were estimated from subsamples

had survival similar to the LOW bed. Furthermore, the LOW and HIH beds had statistically the same size distributions, yet differed in mean annual survival, 98 ± 0.3% and 65 ± 7.8%, respectively (χ^2 = 18.97, df 1, P < 0.0001). Therefore, we believe the size of the mussels in these populations did not contribute to the differences in mean annual survival measured in the present study.

At the initiation of this study in 1995 *Dreissena polymorpha* densities equalled 1700/m² at the HIH bed and increased to over 4100/m² by 1997 (Hart, 1999). *Dreissena polymorpha* colonizations and densities at the LOW and MOD beds in Lake Pepin did not change during this study, remaining near their 1995 levels through 1997 (Hart, 1999). Accordingly, we believe the difference in survival of *Amblema plicata* between the HIH and all other beds was due to the higher levels of *D. polymorpha* colonizations found within the HIH bed.

Ricciardi *et al.* (1995) predicted severe mortality (>90%) when densities of *Dreissena polymorpha* reach about 6000 mussels/m² and 100 *D. polymorpha*/unionid. By comparison, we noted 35% mortality of *Amblema plicata* as *D. polymorpha* densities rose from 1700 to

4100/m² (near the end of the study), and colonization averaged close to 100 *D. polymorpha*/ unionid. The lowered survival of unionids we measured in areas with relatively low numbers of *D. polymorpha* at the MOD bed, ranging from 10–50/m² during this study (Hart, 1999) indicate that populations of colonized mussels are at higher risk than previously docu- mented. Cope *et al.* (1997) reported that some areas of the Mississippi River had densities of *D. polymorpha* averaging over 11,000/m². This density is higher than was measured in the present study (<5000/m²) and would therefore be sure to cause higher unionid mor- tality (Ricciardi *et al.*, 1995)

It is apparent that survival of *Amblema plicata* does not decrease immediately after *Dreis- sena polymorpha* colonization. Survival rates for the *D. polymorpha* colonized HIH population began to decline precipitously 2 y after initial marking and continued to decline throughout the study. Declines in survival rates of the MOD population did not become evident until 2 y after the study began, whereas the survival rates for the LOW and REF populations remained relatively high through 2000. This delayed decline in survival measured at the HIH and MOD beds was also revealed by Haag *et al.* (1993). Haag *et al.*'s (1993) study in Lake Erie revealed that while mortality of *A. plicata* did not increase during their 3 mo experiment, glycogen levels for *D. polymorpha* colonized mussels declined. This lowering of glycogen levels of infested *A. plicata* indicates that energy stores would be reduced over time (Haag *et al.*, 1993; Baker and Hornbach, 2000) and an increase in mortality would occur, thus resulting in the delayed declines in survival rates that we measured in the present study.

Hart (1999) reported the initial occurrence of *Dreissena polymorpha* in Lake Pepin in 1991. Therefore, the marked mussels in the HIH and MOD site were possibly colonized by *D. polymorpha* for at least 4 y before we initiated our study in 1995. It may have taken this long for their accumulated energy stores to fall to levels sufficiently low enough to cause death of the colonized *Amblema plicata* (Haag *et al.*, 1993; Schloesser *et al.*, 1998; Baker and Hornbach, 2000). While we did not measure mortality as high as Ricciardi *et al.* (1995) we believe that as densities of *D. polymorpha* and colonizations of unionids increase in the upper Mississippi River (Hart, 1999) lowered unionid survival will become more evident (Miller and Payne, 2000).

The present study revealed that it may take several years of following individually marked animals to fully measure the effects of *Dreissena polymorpha* on native mussel populations in the Mississippi River system. By directly measuring survival of native mussels in situ in habitats with varying or no *D. polymorpha* infestation we have revealed for the first time that the native mussel species *Amblema plicata* has high natural survival rates and we have provided insight into how quickly these rates can be altered by exotic species invasions.

We recommend that management practices aimed at mitigating the affects of *Dreissena polymorpha* on *Amblema plicata* populations and mussel communities as a whole be imple- mented. While some researchers have advocated the physical removal of *D. polymorpha* from infested unionids as a potential management practice (Schloesser, 1996), this procedure has met with limited success (Schloesser, 1996; Hart *et al.*, 2001). Therefore, a more prom- ising mitigation method may include the translocation of unionids into suitable habitats (Cope and Waller, 1995; Ricciardi *et al.*, 1998) which are at low risk of *D. polymorpha* invasion (Schneider *et al.*, 1998; Kraft and Johnson, 2000).

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